ULTRASTRUCTURE OF THE PRIMARY MALE GENITAL SYSTEM, SPERMATOZOA, AND SPERMIOGENESIS OF *HYPOCHILUS POCOCKI* (ARANEAE, HYPOCHILIDAE)

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Abstract. Spermiogenesis and the ultrastructure of the testes, vasa deferentia, and spermatozoa of *Hypochilus pococki*, a palaeocribellate spider, are described. The sperm exhibit many character states apparently plesiomorphic for spiders (an acrosomal complex composed of a cone-shaped acrosomal vacuole and an acrosomal filament running to the end of a nuclear canal, a postcentriolar nuclear elongation, an axoneme with a 9x2+3 pattern, centrally located mitochondria, and a rolling-up of the nucleus and flagellum at the end of spermiogenesis) and two states that may be synapomorphic for araneomorphs (a stout nucleus and a very pronounced nuclear elongation). The spermatozoa are delivered as cleistospermia (individual spherical sperm cells each encapsulated in a secretory sheath). It is argued that, for spiders, coenospermia are plesiomorphic and cleistospermia apomorphic.

The considerable effort devoted to understanding relationships among spider families has produced varying views on the higher classification of spiders. The most commonly accepted classification scheme is that developed by Platnick and Gertsch (1976) and Platnick (1977), and further supported and developed by Forster et al. (1987) and Coddington (1990). These cladistic analyses favor a classification of spiders into two suborders: Mesothelae and Opisthothelae, with the latter composed of two groups, Mygalomorphae and Araneomorphae. The araneomorphs contain the Paleocribellatae (consisting only of the Hypochilidae) and its sister group, the Neocribellatae (containing all other araneomorphs). Examples of alternative views are those of 1) Lehtinen (1967, 1978, 1986), who has argued that mygalomorphs are more closely related to the Mesothelae than to araneomorphs and that the Araneomorphae is probably not monophyletic (in particular he suggests that a cribellum might have evolved independently in the filistatids) and 2) Eskov and Zonshtein (1990), whose recent cladistic analysis causes them to classify spiders into two suborders which are very different from those of Platnick and Gertsch (1976), i.e.; the Orthognatha (including the Liphistiomorphae, Theraphosomorphae, and Filistatomorphae) and the Labidognatha (including the Geralycosomor-

phae, Dysderomorphae, Hypochilomorphae, and Araneomorphae).

Since the discovery by Franzén (1956) that sperm morphology is correlated with mode of insemination, it has become evident that sperm ultrastructure provides a rich source of characters for testing hypotheses of relationship (see e.g.; Baccetti and Afzelius 1976, Franzén 1977, Afzelius 1979, Baccetti 1979, 1985). Our knowledge of spider sperm ultrastructure has increased considerably since the classic paper of Ōsaki (1969) (Baccetti 1970; Reger 1970; Rosati et al. 1970; Ōsaki 1972; Boissin 1973; Lopez & Boissin 1976; Juberthie et al. 1981; Lopez et al. 1983; Alberti & Weinmann 1985; Alberti et al. 1986). It is of particular interest that four types of sperm packaging have been found in spiders: 1) coenospermia (capsules containing many individual unfused sperm cells), 2) cleistospermia (individual sperm cells, each surrounded by its own sheath), 3) synspermia (several fused sperm cells forming a syncytium which is surrounded by a sheath), and 4) so-called "spermatophores" (tubes of secretion containing a row of highly ordered individual sperm cells) (see Alberti 1990).

Coenospermia have been found electron microscopically in Mesothelae, Mygalomorphae, and Filistatidae (Alberti & Weinmann 1985; Alberti et al. 1986; Alberti 1990). (Although Tuz-

et and Manier [1959] described in the clubionid, *Cheiracanthium* sp., a "spermatophore" which clearly represents a coenospermium, Alberti (1990) could find only cleistospermia in *Cheiracanthium punctorium*.) Synspermia have been observed only in certain haplogyne families (Segestriidae, Dysderidae, Scytodidae, and Loxoscelidae) (Alberti & Weinmann 1985; Alberti (1990). The curious "spermatophores" have only been found in Telemidae (Juberthie et al. 1981), but may also be present in some other families (e.g., Oonopidae, Tetrablemmidae; Brignoli 1978). Cleistospermia have been found in all other araneomorph spiders which have been examined.

The Hypochilidae, which is universally regarded as a primitive taxon and believed by many to be the sister group of all other araneomorph spiders, is of special importance in understanding spider phylogeny. In the following we describe, for the first time, the ultrastructure of spermiogenesis, sperm cells, testes, and vasa deferentia of a hypochilid, *Hypochilus pococki* Platnick, and discuss some of the phylogenetic implications of these results, with special attention to the evolutionary polarity of modes of sperm packaging.

MATERIALS AND METHODS

Three adult males of *H. pococki* were collected on 9 October 1989 near Wolf Creek, 8 km south of Cullowhee, Jackson Co., North Carolina. On 10 October the specimens were dissected and fixed in cold 3.5% glutaraldehyde buffered at pH 7.4 (Sörensen-phosphate buffer) for 2 hours. The fixative was then diluted with buffer solution (1: 4) and in this state the tissues were mailed to Heidelberg where the specimens were rinsed with buffer and postfixed for 2 hours with 2% buffered OsO_4 solution. Following further rinsing with buffer the material was dehydrated with graded ethanols and embedded in Araldite using propylenoxide as an intermedium. Ultrathin sections were obtained using a Reichert OM-U2 ultramicrotome. The sections were stained with uranylacetate and lead citrate and were observed with a Zeiss EM 10CR electron miroscope.

RESULTS

Testes.—The massive, elongate paired testes are located ventrally in the opisthosoma. Spermiogenesis begins in cysts containing numerous germ cells in the same stage of development. Later the cysts become less compact and may be confluent (Figs. 1, 2). These cysts are formed by

extensions of large somatic cells characterized by their irregular shape, interdigitations with neighboring somatic cells, and numerous desmosomes (Figs. 3–5, 24). Each somatic cell also contains a large, irregularly shaped, electron lucent nucleus, numerous conspicuous cisternae of rough ER, dictyosomes, several small mitochondria, and various inclusions which are probably lysosomes. Some somatic cells are quite dense and show signs of degeneration (dilated ER cisternae, disintegrating cell apex, etc.) (Fig. 4). Narrow extensions of the somatic cells reach between germ cells only in an early stage of development. Each testis is underlain by a thick basal lamina supported by a similarly thick layer of collagenous fibres, and a muscularis adjacent to the haemocoel (Fig. 3).

Vasa deferentia.—In the proximal parts of the vasa deferentia, which are continuous with the distal parts of the testes, the epithelial cells are similar to the somatic cells of the testes, and the basal components (basal lamina, collagenous layer, muscularis) are similarly present. The lumen of the proximal region contains a homogeneous secretion and coiled spermatozoa which are not yet surrounded by a secretory sheath. This encystment occurs in the distal vas deferens where the secretory activity is much higher. The lumen here in the distal portion is filled with a densely staining material, aggregates of granules and spheres, and streaks which probably consist of the same material that forms the sheaths of the sperm cells (Figs. 6, 10). Large nuclei with folded surfaces, cisternae of rough ER, many dictyosomes, and secretory vesicles are conspicuous in the epithelial cells. The apical surface of these cells is provided with microvilli with many small vesicles at their bases. Laterally these cells are connected by extensive junctional complexes (Fig. 6). The basal plasmalemma of the cells is folded and attached via hemidesmosomes to a rather thin basal lamina (Fig. 7). The collagenous layer is also thinner than in the testis. Within the muscularis are many nerve endings (Fig. 8).

Spermatozoa.—The mature spermatozoa found in the distal vas deferens are spherical (Fig. 9) and each one is encapsulated in a multilayered 0.3 μm thick secretory sheath. The following structures are observable in each sperm cell:

Acrosomal complex: The acrosomal complex is composed of an acrosomal vacuole (or vesicle) in the shape of an elongate hollow cone and an acrosomal filament (Figs. 11, 12). The acrosomal vacuole is located at the anterior end
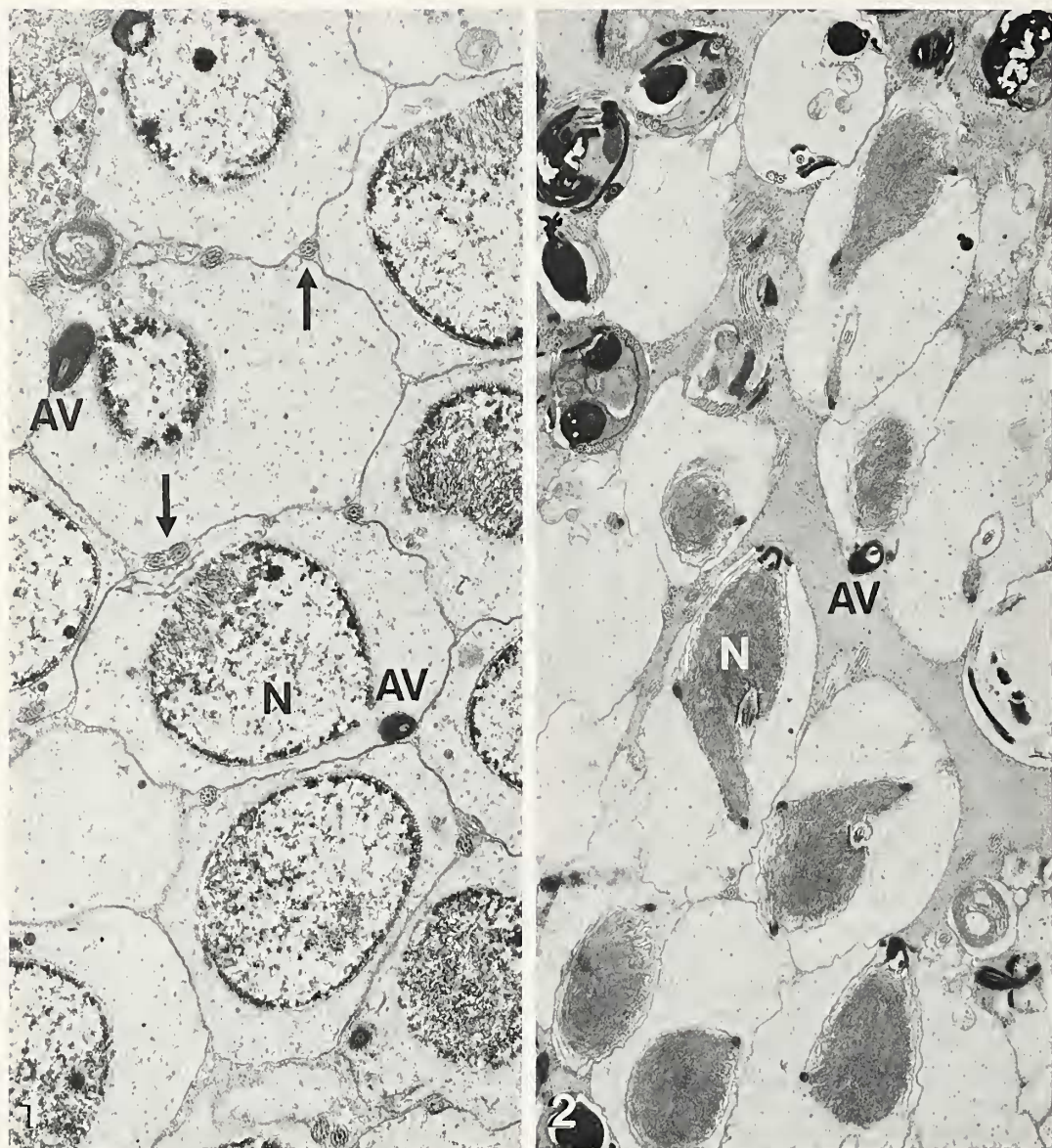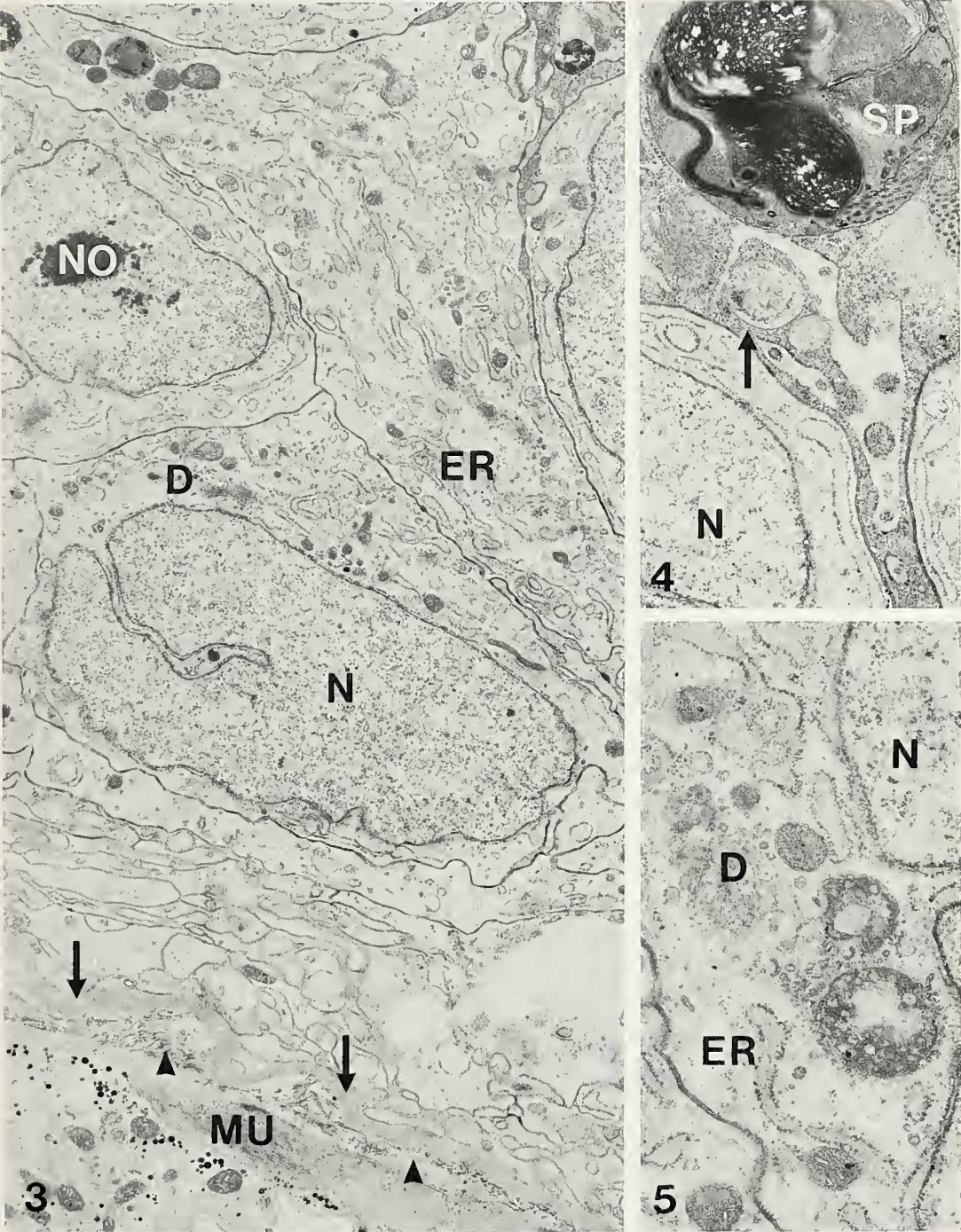
Figures 1, 2.—Spermiogenesis in *Hypochilus pococki*: 1, part of a cyst within the testis containing spermatids in a very early stage of spermiogenesis. Note that cells are densely packed (arrows point to flagella of spermatids located within narrow intercellular clefts). Chromatin condensation has just started. Acrosomal vacuoles are already dense. X6,300. 2, advanced stages of spermiogenesis (compare Fig. 20). Cytoplasm of the spermatids is rather electron lucent. Note extensive intercellular spaces between spermatids and nearly mature spermatozoa (upper left). X4,000. AV = acrosomal vacuole, N = nucleus.

of the nucleus, runs parallel to the cell surface, and does not protrude from the cell body. The contents of the acrosomal vacuole are rather homogeneous and electron dense; only the innermost region shows distinct layers (Fig. 12). The acrosomal filament, composed of many (actin?) subfibers (Figs. 12, 22, 23), is rather thick and

runs through the subacrosomal space into the nuclear canal down to its end (Figs. 11, 13).

Nucleus: The nucleus is the most prominent structure of the sperm cell and is bent upon itself. The main part of the nucleus is rather stout, it describes approximately two-thirds of a circle within the capsule (Fig. 9), and its convex pe-

Figures 3–5.—Spermiogenesis in *Hypochilus pococki*: 3, somatic cells from the testis close to proximal part of vas deferens. Arrows point to basal lamina, arrow heads to collagenous layer. X6,300. 4, margin of cyst which contains nearly mature spermatozoon. Note dense (degenerating) somatic cell (arrow). X12,600. 5, dictyosome and rough ER close to nucleus of somatic cell. X20,000. D = dictyosome, ER = rough endoplasmic reticulum, MU = muscle cell, N = nucleus, NO = nucleolus, SP = spermatozoon.
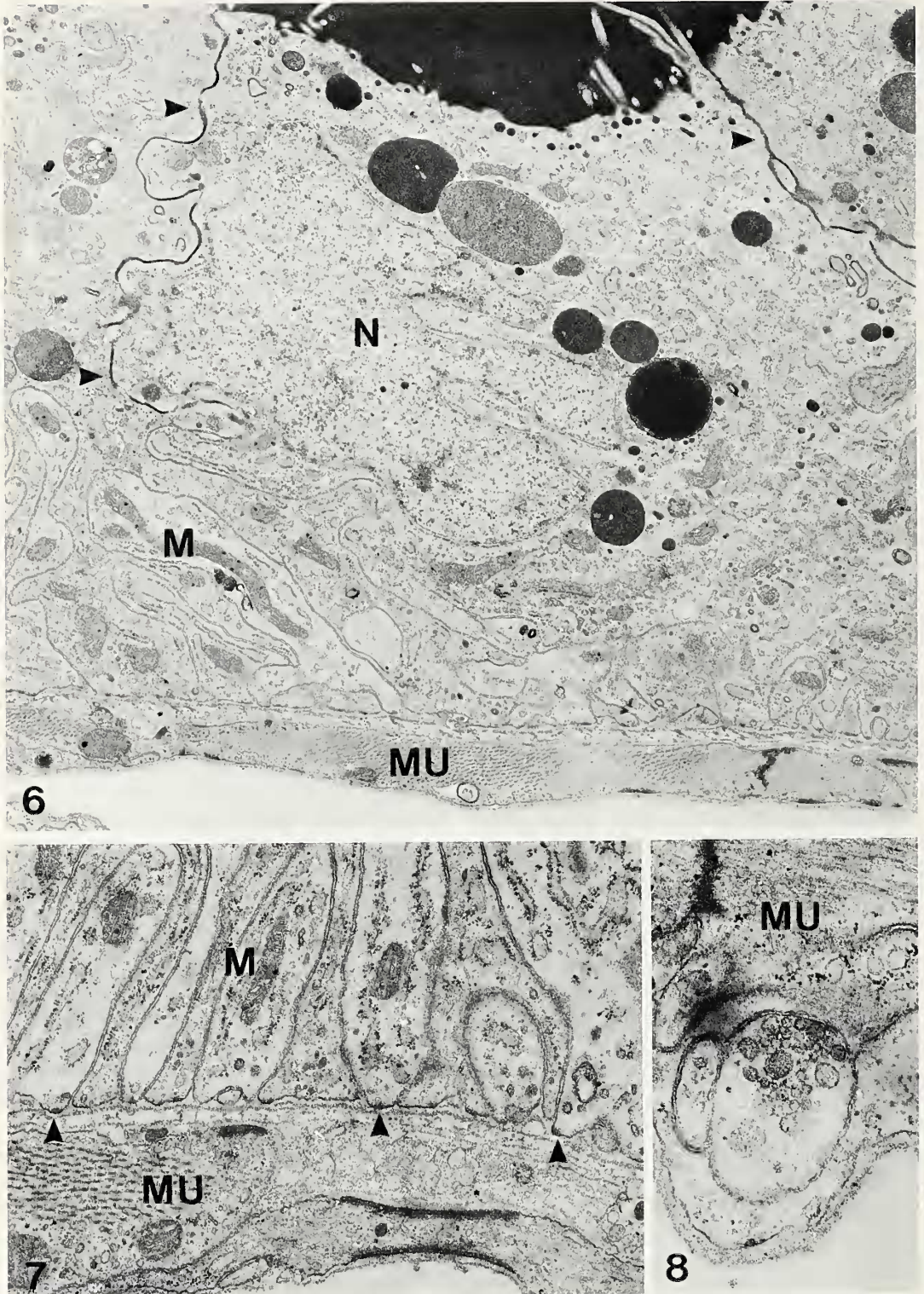
Figures 6–8.—Spermiogenesis in *Hypochilus pococki*: 6, distal vas deferens containing dense secretion. Note irregularly shaped nucleus, numerous vesicles, and extensive cell junctions (arrow heads). X9,450. 7, basal region

ripheral surface is smooth whereas its concave, centrally directed surface is folded. The nucleus extends beyond the axonemal base as a flattened, so-called postcentriolar, nuclear elongation which completes the circle and continues parallel to the acrosomal vacuole reaching even behind the axonemal base (Figs. 9, 11, 13). The nuclear elongation is thus rather long (about one complete circle). The close apposition of the nuclear elongation to the acrosomal vacuole is quite distinctive (Figs. 11, 13). The nucleus contains a peripheral canal which curves around its whole length and contains the acrosomal filament (Figs. 11, 13).

Axonema: The implantation fossa, which is moderately deep, includes, in front of the centrioles, a homogeneous material (centriolar adjunct) and numerous small granules, presumably glycogen (Figs. 9, 11, 13). The axonemal base is marked by dense material which is opposed to the peripheral tubules (Figs. 14, 16). The center of the distal centriole includes three dense fibers which are continuous with the dense material connecting the three central tubules of the axonema, which thus exhibits the 9x2+3 pattern typical for most spiders (Figs. 14–17). The axonema, which lacks a flagellar membrane, describes four to five coils within the cell body (Figs. 13, 17). The A-tubules are denser proximally than distally (Fig. 17). Only in the very distal part of the axonema are the central tubules lacking.

Additional components: Some mitochondria are found in the center of the cell together with irregularly arranged dense streaks (Figs. 9, 11, 13). These streaks are probably condensed membranes as is indicated by younger stages of sperm development (see below; Fig. 24). Regions of cytoplasm devoid of organelles are studded with moderately dense granules, which most likely represent β-glycogen (Fig. 9).

Spermiogenesis.—Young spermatids at the beginning of chromatin condensation are densely packed cells with spherical nuclei. The acrosomal vacuole was already present in the stages we observed and is located opposite a region of the nucleus where chromatin condensation starts (Figs. 1, 18). The acrosomal vacuole is slightly inclined against the long axis of the cell and the acrosomal filament thus runs obliquely into the nuclear canal (Fig. 18). The nucleus is surrounded by a manchette of microtubules. Opposite the acrosomal vacuole the nucleus invaginates to form the implantation fossa (Figs. 19, 21). At this pole of the cell, the mitochondria have assembled. The flagellum extends into the intercellular clefts left between the developing spermatids which are interconnected by narrow cell bridges (Fig. 1). Some extensions of somatic cells are also visible between the spermatids.

In a later stage, the nucleus narrows somewhat towards its anterior end (Fig. 19). The acrosomal vacuole is basally surrounded by a girdle of dense material to which the manchette microtubules are attached (Figs. 20, 22). The implantation fossa is quite deep and includes the centrioles in a tandem orientation (Fig. 21). The chromatin is filamentous now. The surface of the cell becomes irregular and between the cells are found more extensive intercellular spaces containing a heterogeneous material (Figs. 2, 20). It appears as if large quantities of cytoplasmic material are discarded from the spermatids, predominately from those regions which are close to the cell bridges. These discarded "blebs" often include large complexes of cisternae in different stages of destruction (Fig. 21).

In this stage the cells have already elongated and the nucleus exhibits a prominent nuclear elongation (Fig. 20). The flagellum is partly sunken into the cell and is consequently surrounded by an invagination of the flagellum to form a so-called flagellar tunnel (Figs. 20, 23). The nuclear envelope shows distinct nuclear pores in its posterior part (Figs. 19, 20). The acrosomal vacuole is somewhat more dense, and the nuclear canal with the acrosomal filament is complete, appearing as a prominent ridge on the surface of the nucleus (Figs. 20, 21, 24). The mitochondria are still located at the posterior end of the cell. The cytoplasm is rather electron lucent, including only few dense granules. Remarkably, we did

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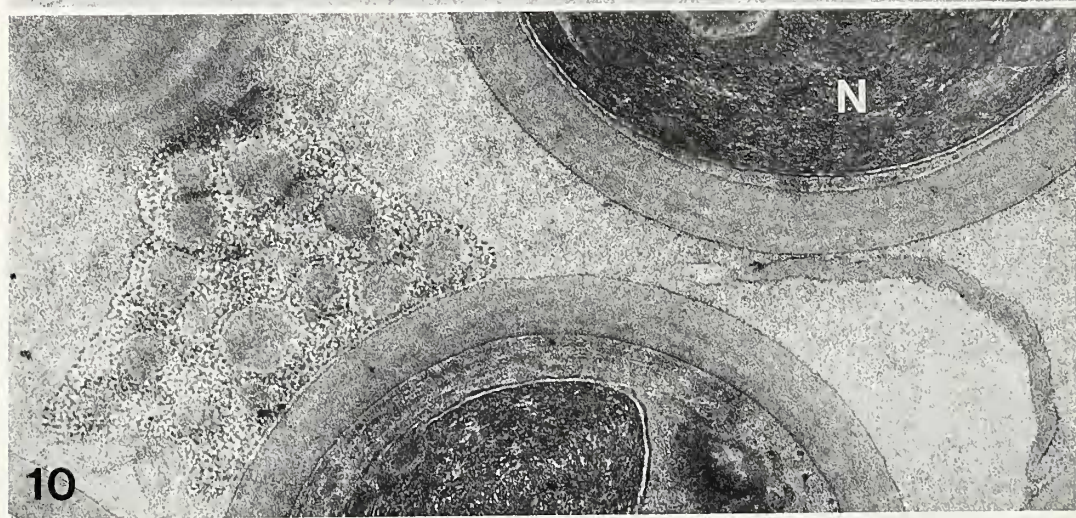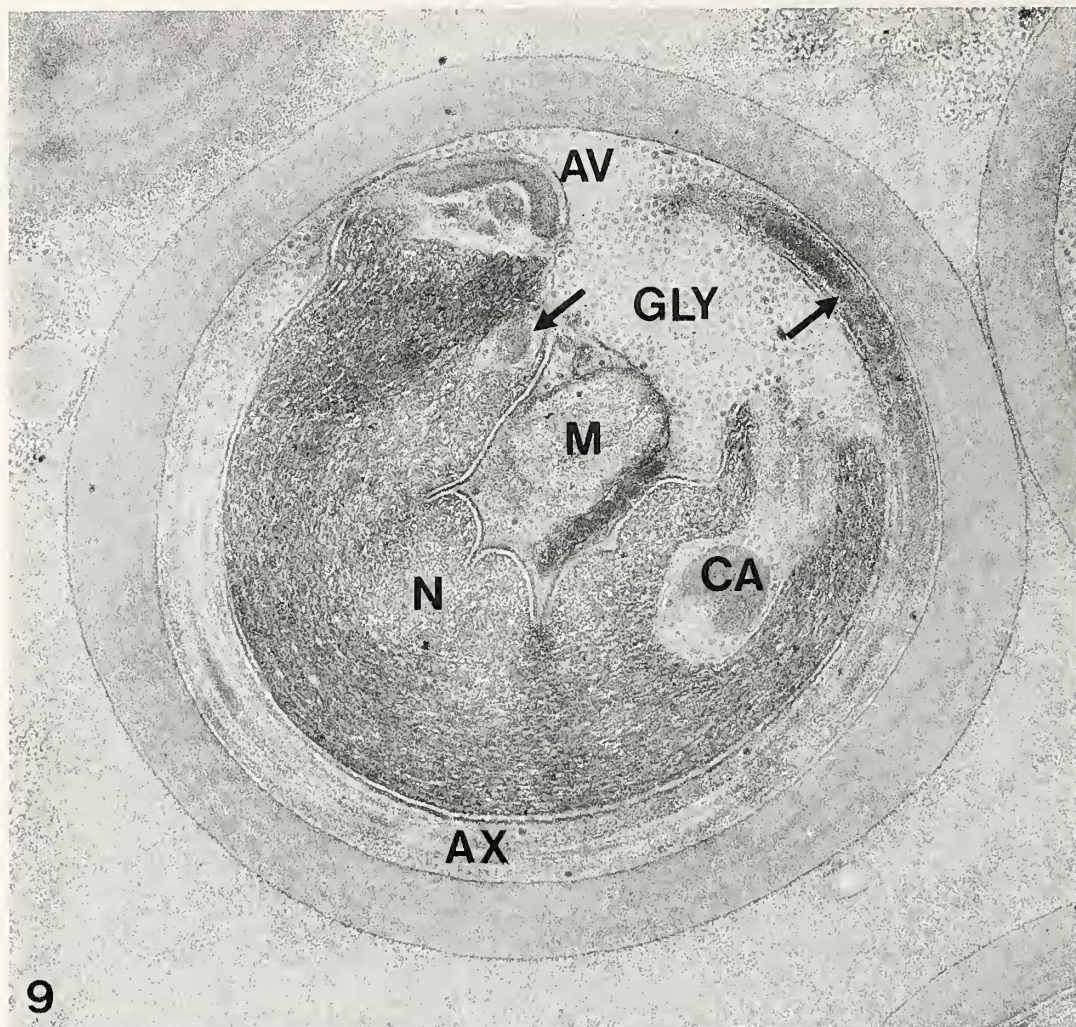
Figures 9, 10.—Spermatozoa of *Hypochilus pococki*: 9, mature coiled spermatozoon within lumen of distal vas deferens. Note multilayered secretory sheath. Arrows point to acrosomal filament. X32,000. 10, different secretions within vas deferens. X25,000. AV = acrosomal vacuole, AX = axonema, CA = centriolar adjunct within implantation fossa, GLY = glycogen, M = mitochondrion, N = nucleus.
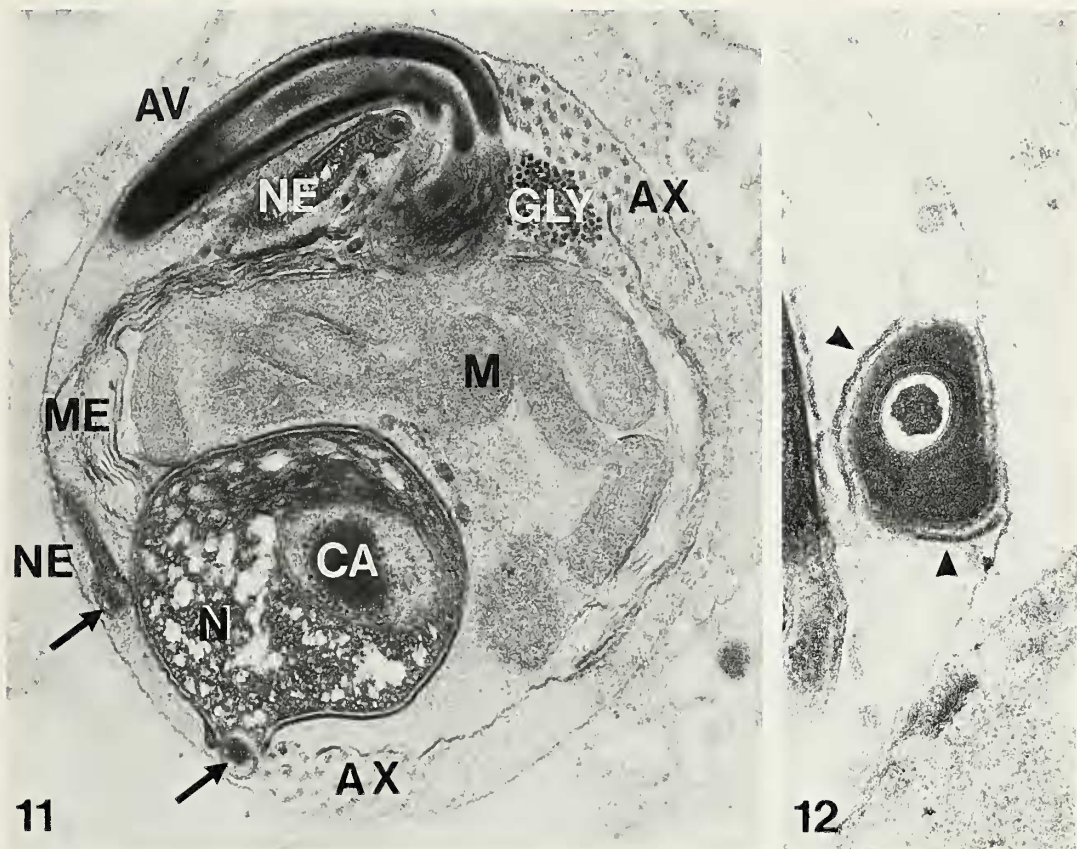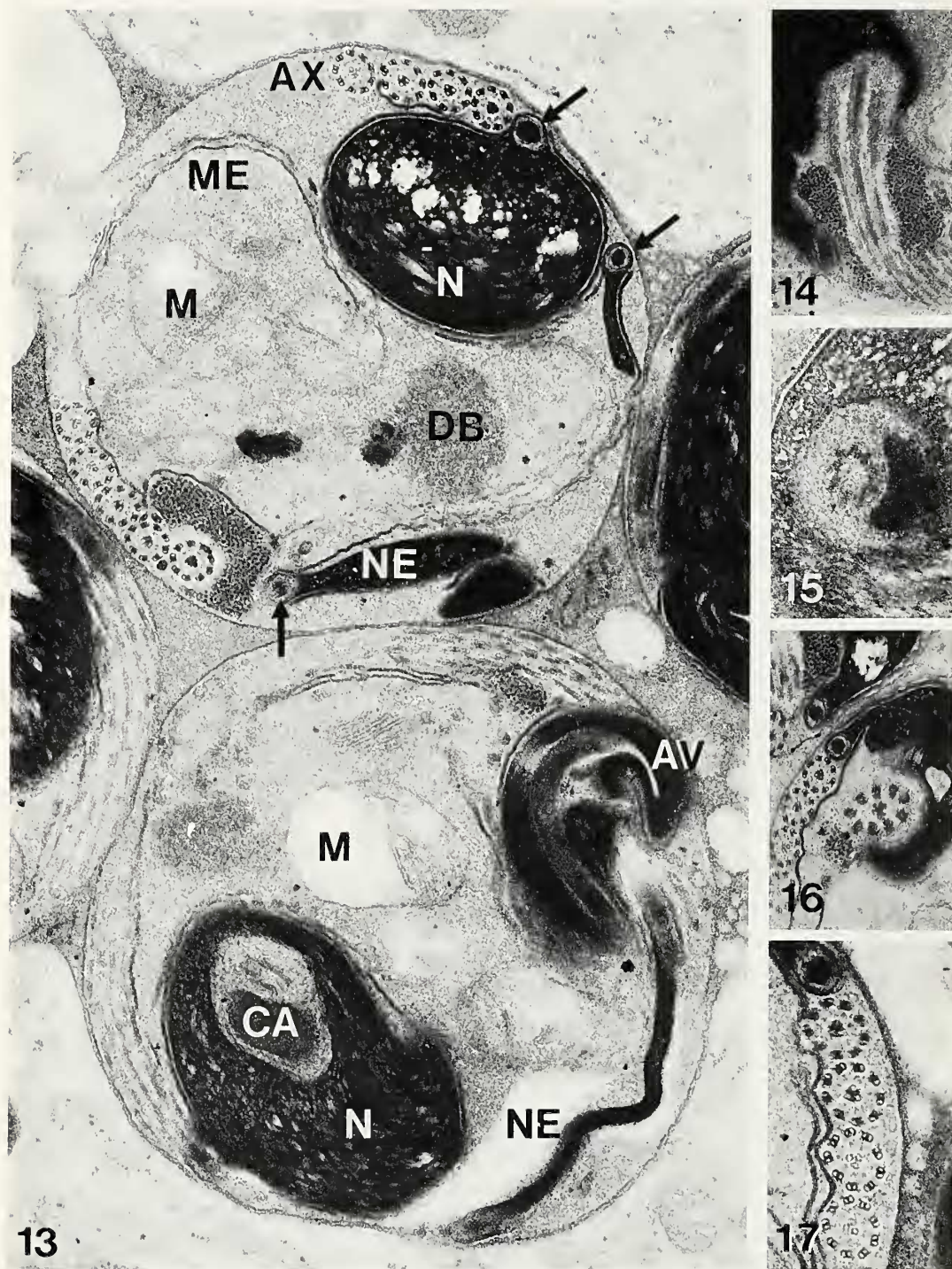
Figures 11, 12.—Spermatozoa of *Hypochilus pococki*: 11, nearly mature spermatozoon from testis. Note acrosomal vacuole sectioned longitudinally, postcentriolar nuclear elongation, centriolar adjunct within implantation fossa, numerous mitochondria, membranes and cisternae, glycogen, and axonema. Arrows point to acrosomal filament. X30,000. 12, transverse section through acrosomal complex. Note concentric layers within acrosomal vacuole close to subacrosomal space containing acrosomal filament, which is composed of subfibers. Dense cisternae are opposed to acrosomal vacuole (arrow heads). X60,000. AV = acrosomal vacuole, AX- = axonema, CA = centriolar adjunct, GLY = glycogen, M = mitochondrion, ME = membranes, N = nucleus, NE = nuclear elongation.

not observe any membranous material within the cytoplasmic matrix in this or earlier stages (Figs. 2, 20).

Finally the chromatin condenses completely to an almost totally dark structure leaving extensive areas of electron lucent nucleoplasm surrounded by the nuclear envelope (Fig. 23). Also in this stage there are no (other) membranes present within the cytoplasmic matrix; these only appear after the coiling process, which presumably occurs rapidly since no intermediate stages were found. In these nearly mature sperm cells distinct dense cisternae were found, some of which parallel the nucleus and acrosomal vacuole (Figs. 24, also 11, 13). The cytoplasm is rather homogeneous but some (glycogen?) granules are already concentrated at the axonemal base (Figs. 11, 13). Further, in the center of the cell is established a "dense body", which later becomes unrecognizable because of the general condensation of the cytoplasm (Figs. 24, also 13). The flagellum is completely incorporated, i.e., the axonema is without a flagellar membrane (Figs. 24, also 11, 13, 17). The cell further condenses and finally achieves the stage of the mature spermatozoon. The cysts open and the sperm cells, together with the intercellular fluid, are expelled into the lumen of the testis, which is established by such confluent cysts and is continuous with the lumen of the vas deferens.

Figures 13–17. — Spermatozoa of *Hypochilus pococki*: 13, two nearly mature spermatozoa from testis. Note dense nuclei with nuclear elongation and nuclear canal containing acrosomal filament (arrows). Membranes and cisternae in part are parallel with nucleus. X20,000. 14, longitudinal section through axonemal base showing modified distal centriole with central axis and proximal part of axoneme surrounded by glycogen. X20,000. 15–17, transverse sections: 15, proximal centriole within implantation fossa closely attached to centriolar adjunct. X37,500. 16, axonemal base with central axis. Note accessory dense elements opposed to peripheral tubules.

DISCUSSION

The sperm cells of *H. pococki* are quite similar to those of many other araneomorph spiders (Alberti 1990). Based upon observations of spermatozoa in other spiders (including *Filistata insidiatrix* Forskal) and pedipalpate arachnids (Uropygi and Amblypygi), we believe that two of these similarities (the stout nucleus and the very pronounced nuclear elongation) may be regarded as araneomorph synapomorphies and are therefore supportive of Platnick and Gertsch's (1976) phylogeny. Many other *Hypochilus* character states appear to be plesiomorphic, e.g., the presence of several mitochondria, membranous material and a "dense body", the high number of glycogen granules, the rather simple implantation fossa, the cone-shaped acrosomal vacuole, and the acrosomal filament extending through the whole length of the nuclear canal. These states are also found in *F. insidiatrix* and many (other) araneomorph spiders as well as in mygalomorphs, liphistiomorphs, and pedipalpate arachnids (Alberti & Weinmann 1985; Alberti et al. 1986; Alberti 1990; Ōsaki 1969; Phillips 1976; Jespersen 1978; Tripepi & Saita 1985; Alberti & Palacios-Vargas 1987). Thus our findings are consistent with the interpretation that Hypochilidae are ancient araneomorph spiders.

The discovery of cleistospermia in the hypochilids leads us back to the question, first discussed by Bertkau (1877, 1878), of whether cleistospermia or coenospermia are plesiomorphic for spiders. Since only individual (not aggregated) sperm cells have been found in uropygids and amblypygids (the presumed sister group of spiders), outgroup comparison supports the hypothesis that cleistospermia are plesiomorphic. If this is true, then coenospermia could be a synapomorphy uniting the liphistiids, mygalomorphs, and filistatids (the only araneomorph taxon in which coenospermia have been found electron microscopically), a pattern consistent with some of Lehtinen's (1978) ideas and Eskov and Zonshtein's (1990) phylogeny.

If, on the other hand, coenospermia are primitive for spiders, as Alberti & Weinmann (1985), Alberti et al. (1986), and Alberti (1990) have argued, cleistospermia could be a synapomorphy for araneomorphs (with reversals in the filistatids and *Cheiracanthium* sp.) or, more likely, cleistospermia could have arisen two or more times independently in the Araneomorphae. We favor the hypothesis that coenospermia are plesiomorphic for spiders for the following reasons: 1) Coenospermia have been found predominately in spiders which are "primitive." 2) Although not found in amblypygids and uropygids, aggregations of spermatozoa comparable to coenospermia are found in other arachnids (scorpions, solpugids, opilionids, and certain mites) (Alberti 1990). 3) Given our current knowledge of the distribution of coenospermia and cleistospermia, and if, as our above-mentioned synapomorphies suggest, the phylogeny of Platnick and Gertsch (1976) is correct, it is more parsimonious to hypothesize that coenospermia is the primitive state (character state changes are required only within the Araneomorphae) than that it is derived (changes are required in the Mesothelae, Mygalomorphae, and Araneomorphae).

Other issues relevant to the evolution of modes of sperm packaging deserve comment. First, the observation that many cleistospermia are rather similar to coenospermia, particularly with respect to the (often multilayered) secretory sheath and cellular components, and especially when compared with the coenospermia of *F. insidiatrix*, suggests that the evolutionary shift from coenospermia to cleistospermia may be achieved easily. The presence of coenospermia in one species of *Cheiracanthium* (Tuzet & Manier 1959) and of cleistospermia in another (Alberti 1990) also supports this hypothesis. Secondly, although it is tempting to hypothesize that the syncytial synspermia of some haplogynes and the multicellular "spermatophores" of the telemids have evolved from the multicellular coenospermia, both types could also represent aggregates which have originated independently from cleistospermia (see Alberti 1990). Finally, in spite of the greater amount of secretory sheath material needed to package a given number of sperm as cleistospermia rather than as coenospermia,

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X24,000. 17, coiled axonema incorporated within cell body showing 9x2+3 pattern of tubules. In proximal part of axonema, A-tubules are densely staining and central tubules are interconnected by dense material. X40,000. AV = acrosomal vacuole, AX = axonema, CA = centriolar adjunct, DB = dense body, M = mitochondrion, ME = membranes, N = nucleus, NE = nuclear elongation.
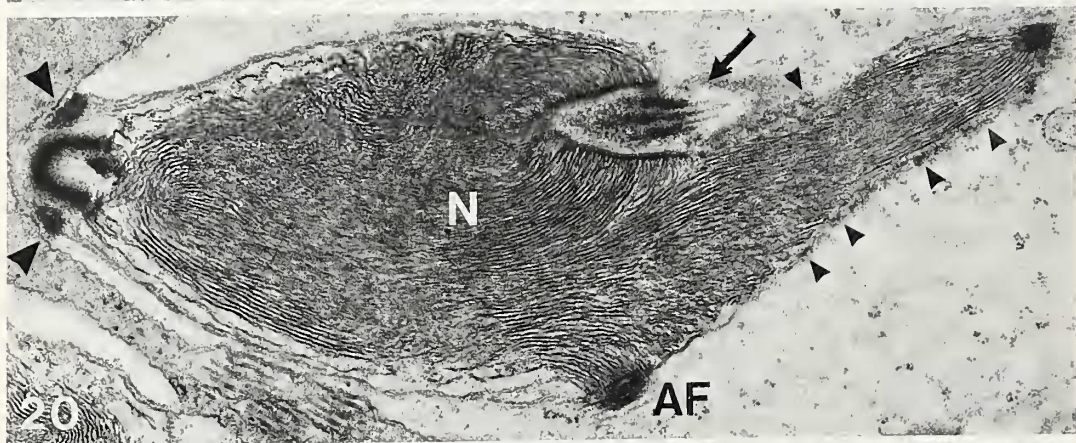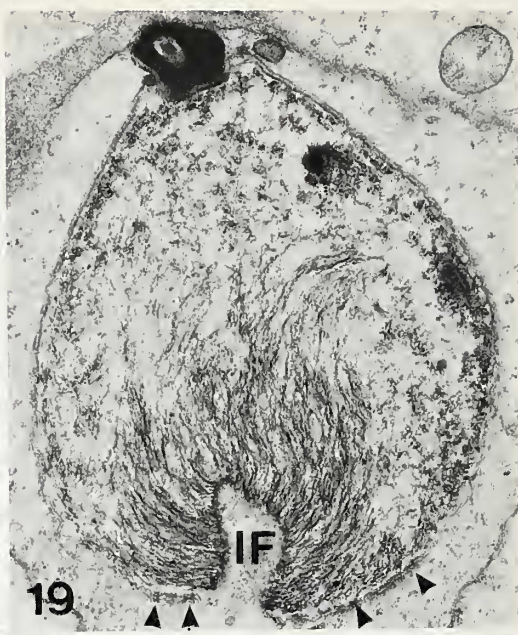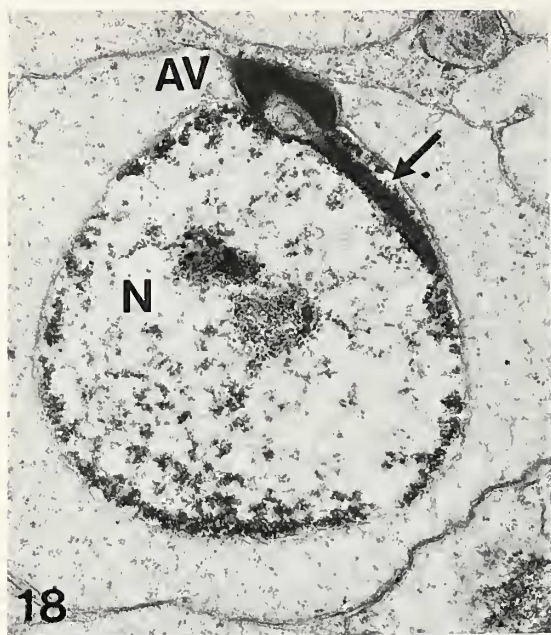
Figures 18–21. — Details of spermiogenesis in *Hypochilus pococki*: 18, early stage with acrosomal vacuole inclined to longitudinal axis of nucleus. Acrosomal filament (arrow) runs obliquely into nuclear canal. X12,600. 19, advanced stage with implantation fossa. Note nuclear pores at posterior part of nucleus (arrow heads). Fibrillar chromatin condensation starts in posterior part of nucleus. X12,600. 20, more advanced stage. Chromatin is completely fibrillar. A prominent postcentriolar nuclear elongation has developed. Note flagellar base with flagellar tunnel sectioned only in its proximal part (arrow). Small arrow heads indicate nuclear pores. Nucleus is provided with manchette microtubules attached to a dense girdle around the acrosomal vacuole (large arrow
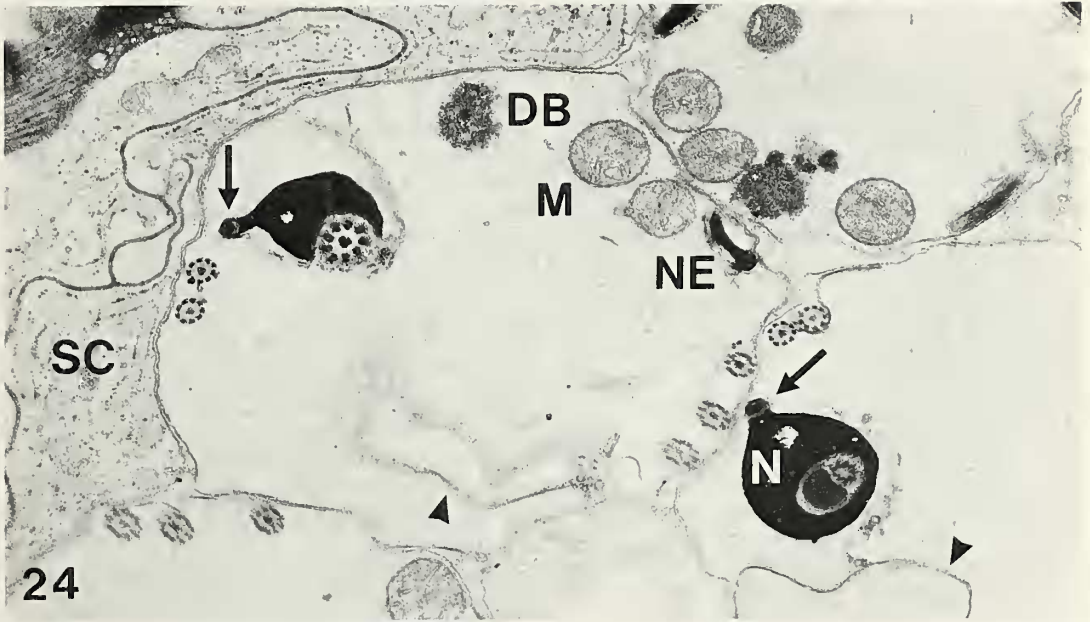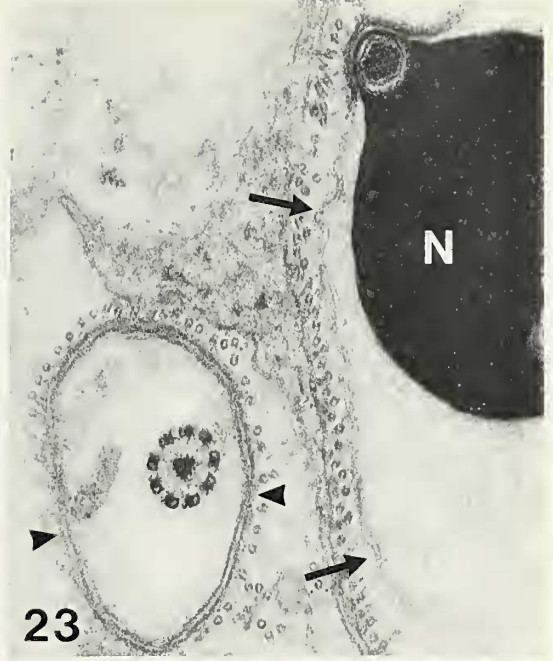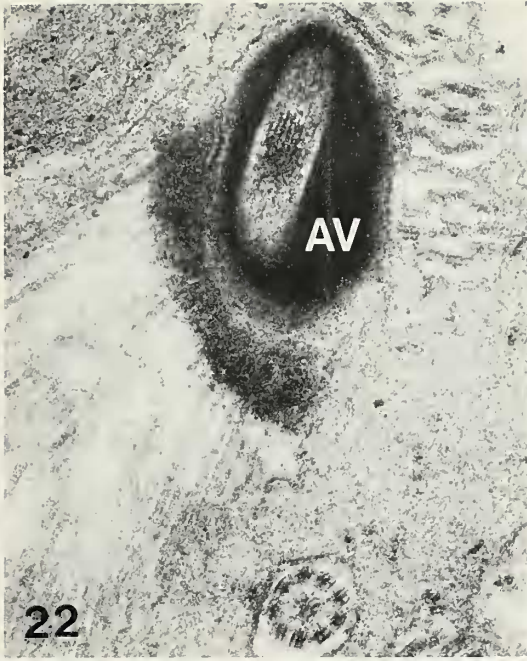
Figures 22–24.—Spermatids of *Hypochilus pococki*: 22, tangentially sectioned acrosomal complex showing acrosomal vacuole and acrosomal filament, composed of subfibers. Dense girdle with attached manchette microtubules. X48,000. 23, transverse section through flagellar tunnel around proximal part of flagellum (arrow heads) of a spermatid. Note manchette microtubules. Arrow indicates nuclear envelope. X48,000. 24, spermatids shortly after coiling and not completely condensed (note only 2 and 3 transverse sections of the axonema within the cell in center of figure). Within cytoplasm dense cisternae are apparent now (arrow heads). Arrows point to acrosomal filament. X12,600. AV = acrosomal vacuole, DB = dense body, M = mitochondrion, N = nucleus, NE = nuclear elongation, SC = somatic cell.

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heads). X16,000. 21, same stage as in Fig. 20 showing implantation fossa with centrioles in tandem position. At right a cytoplasmic "bleb" containing irregular membranous network is detached from cell bridge region. X16,000. AF = acrosomal filament, AV = acrosomal vacuole, CB = cell bridge, IF = implantation fossa, N = nucleus.

transferring sperm as cleistospermia may be generally more effective, particularly in araneomorph genitalia, which often have narrower and more sharply bent ducts than do nonaraneomorph genitalia. Cleistospermia are smaller than coenospermia and therefore should be able to move through such ducts with less resistence and less chance of becoming stuck. A study of the degree of correlation between sperm packet diameter and genital duct diameter in spiders might help test for such a functional relationship, one which could play an important role in the evolution of sperm packaging.

Spider sperm ultrastructure is evidently a rich source of characters. As more taxa are examined and as more is learned about the functional morphology of spider genitalia (and therefore, perhaps, the selective advantage of different types of sperm), it may be possible to learn much about spider phylogeny from comparative spermatology.

LITERATURE CITED

Afzelius, B. A. 1979. Sperm structure in relation to phylogeny in lower metazoa. Pp. 243–251, *In* The Spermatozoan. (D. W. Fawcett & J. M. Bedford, eds.). Urban and Schwarzenberg, Baltimore-Munich.

Alberti, G. 1990. Comparative spermatology of Araneae. Acta Zool. Fenn., 190:17–34.

Alberti, G., B. A. Afzelius & S. M. Lucas. 1986. Ultrastructure of spermatozoa and spermatogenesis in bird spiders (Theraphosidae, Mygalomorphae, Araneae). J. Submicrosc. Cytol., 18:739–753.

Alberti, G. & J. G. Palacios-Vargas. 1987. Fine structure of spermatozoa and spermatogenesis of *Schizomus palaciosi*, Reddell and Cokendolpher, 1986. (Arachnida: Uropygi: Schizomida). Protoplasma, 137:1–14.

Alberti, G. & C. Weinmann. 1985. Fine structure of spermatozoa of some labidognath spiders (Filistatidae, Segestriidae, Dysderidae, Oonopidae, Scytodidae, Pholcidae; Araneae; Arachnida) with remarks on spermiogenesis. J. Morphol., 185:1–35.

Baccetti, B. 1970. The spermatozoa of Arthropoda. IX. The sperm cell as an index of arthropod phylogeny. Pp. 169–181, *In* Comparative Spermatology. (B. Baccetti, ed.). Academic Press, Orlando.

Baccetti, B. 1979. Ultrastructure of sperm and its bearing on arthropod phylogeny. Pp. 609–644, *In* Arthropod Phylogeny. (A. P. Gupta, ed.) Van Nostrand Reinhold, New York.

Baccetti, B. 1985. Evolution of the sperm cell. Pp. 3–58, *In* Biology of Fertilization. Vol. 2. Biology of the Sperm. (C. B. Metz & A. Monroy, eds.). Academic Press, Orlando.

Baccetti, B. & B. A. Afzelius. 1976. The Biology of the Sperm Cell. Monographs in Developmental Biology. Vol. 10. Karger, München.

Bertkau, P. 1877. Über die Übertragungsorgane und die Spermatozoan der Spinnen. Verh. Naturh. Ver. preuss. Rheinl., 34:28–32.

Bertkau, P. 1878. Versuch einer natürlichen Anordnung der Spinnen nebst Bemerkungen zu einzelnen Gattungen. Arch. f. Naturgesch., 44:351–410.

Boissin, L. 1973. Etude ultrastructurale de la spermiogenese de *Meta bourneti* Simon (Arachnides, Araneides, Metinae). C.R. 2e Réun. Arachnol. Exp. franc., Montpellier, 1973:7–22.

Brignoli, P. M. 1978. A few notes on a remarkable South African troglobiotic spider, *Congoderes lewisi* Harington, 1951 (Araneae, Telemidae). Rev. Suisse Zool., 85:111–114.

Coddington, J. A. 1990. Ontogeny and homology in the male palpus of orb-weaving spiders and their relatives, with comments on phylogeny (Araneoclada: Araneoida, Deinopoidea). Smithson. Contrib. Zool., (496):1–52.

Eskov, K. Y. & S. L. Zonshtein. 1990. A new classification for the order Araneida (Arachnida: Chelicerata). Acta Zool. Fenn., 190:129–137.

Forster, R. R., N. I. Platnick & M. R. Gray. 1987. A review of the spider superfamilies Hypochiloidea and Austrochiloidea (Araneae, Araneomorphae). Bull. Amer. Mus. Nat. Hist., 185:1–116.

Franzén, A. 1956. On spermiogenesis, morphology of the spermatozoon, and biology of fertilization among invertebrates. Zool. Bidrag., Uppsala, 31:255–482.

Franzén, A. 1977. Sperm structure with regard to fertilization biology and phylogenetics. Verh. Dtsch. Zool. Ges., 1977:123–138.

Jespersen, A. 1978. The fine structure of spermiogenesis in the Amblypygi and Uropygi (Arachnida). Zoomorphol., 89:237–250.

Juberthie, C., A. Lopez & J. Kovoor. 1981. Spermiogenesis and spermatophore in *Telema tenella* Simon (Araneae: Telemidae) - An ultrastructural study. Int. J. Invert. Reprod., 3:181–191.

Lehtinen, P. T. 1967. Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. Ann. Zool. Fenn., 4:199–468.

Lehtinen, P. T. 1978. Definition and limitation of supraspecific taxa in spiders. Symp. Zool. Soc. London, 42:255–271.

Lehtinen, P. T. 1986. Evolution of the Scytodoidea. Pp. 149–157, *In* Proc. 9th Intern. Congr. Arachnol. (W. G. Eberhard, Y. D. Lubin & B. C. Robinson, eds.). Smithsonian Inst. Press, Washington, D. C.

Lopez, A. & L. Boissin. 1976. La spermatide d'*Holocnemus pluchei* (Scop.) (Arachnida, Araneida, Pholcidae): Etude ultrastructurale. Bull. Soc. Zool. France, 101:423–431.

Lopez, A., J.-C. Bonaric, & L. Boissin. 1983. Etude

ultrastructurale de la spermiogenese chez l'araignée *Pisaura mirabilis* (Clerck, 1858) (Pisauridae). Rev. Arachnol., 5:55–64.

Ōsaki, H. 1969. Electron microscope study on the spermatozoon of the liphistiid spider, *Heptathela kimurai*. Acta Arachnol., 22:1–12.

Ōsaki, H. 1972. Electron microscope study on spermiogenesis in the spider, *Oxyopes sertatus*. Japan. J. Zool., 16:184–199.

Phillips, D. M. 1976. Nuclear shaping during spermiogenesis in the whip scorpion. J. Ultrastr. Res., 54:397–405.

Platnick, N. I. 1977. The hypochiloid spiders: a cladistic analysis, with notes on the Atypoidea (Arachnida, Araneae). Amer. Mus. Novitates, (2627):1–23.

Platnick, N. I. & W. J. Gertsch. 1976. The suborders of spiders: a cladistic analysis. Amer. Mus. Novitates, (2607):1–15.

Raven, R. J. 1985. The spider infraorder Mygalomorphae: cladistics and systematics. Bull. Amer. Mus. Nat. Hist., 182:1–180.

Reger, J. F. 1970. Spermiogenesis in the spider *Pisaurina* sp.: a fine structure study. J. Morphol., 130: 421–434.

Rosati, F., B. Baccetti & R. Dallai. 1970. The spermatozoa of Arthropoda. X. Araneids and the lower myriapods. Pp. 247–254, *In* Comparative Spermatology. (B. Baccetti, ed.) Academic Press, New York.

Tripepi, S. & A. Saita. 1985. Ultrastructural analysis of spermiogenesis in *Admetus pomilio* (Arachnida, Amblypygi). J. Morphol., 184:111–120.

Tuzet, O. & J. F. Manier. 1959. Recherches sur la spermiogenese des araignées: *Araneus cornutus, Tetragnatha pinicola, Philodromus poecilus*, et *Chiracanthium* sp. Ann. Sc. Nat. Zool., 12e ser.:91–103.